MORPHOLOGICAL AND ECOLOGICAL CONSIDERATIONS IN THE CLASSIFICATION OF NAVARRETIA (POLEMONIACEAE)

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Ruiz and Pavon (1799) erected the genus *Navarretia* upon *N. involucrata,* the only species of the genus occurring in South America. Mason (1951) recognizes twenty-nine species of the genus occurring in Western North America and centering chiefly in California. It is the purpose of this paper to examine more closely some of the morphological and ecological features of these species as an aid to increased understanding of their interrelationships. All species were studied from herbarium specimens at the University of California at Berkeley, the author's collections, and in some instances cultivated material. Specific reference to any particular plant material has been made only when exceptional variations are worthy of note or limited material warrants citation.

Morphological Criteria

The possible evolutionary significance of several morphological features, mainly floral, became evident during this investigation. Among these, corolla venation, stamen insertion, stigma lobing, capsule modifications, seed number, glands, and vessel anatomy, will be discussed in turn.

1. Corolla Venation

The vascular supply to the corolla may be readily observed. Flowers from herbarium specimens or living plants are allowed to become fully soaked in water on a glass slide, a very simple process which is sufficient for clearing, and adequate to reveal the vascular system. The use of a dark background on a binocular dissecting microscope and careful longitudinal slitting of the corolla tube exposes the complete vasculation pattern and clearly shows the position of stamens and style. Stamen vasculation is similar throughout the genus, the stamens always being supplied by single veins which alternate with the petal veins. Inasmuch as significant variation is lacking, stamen vasculation is omitted in the following discussion.

Corolla vasculation, other than that supplying the stamens, has been found, however, to be of significance. With the exception of the South American *N. involucrata, Navarretia* may be divided into those species having trinervate vasculation and those having uninverate vasculation of the corollas. Twenty-one species fall into the trinervate group wherein a single vein for each lobe enters the base of the corolla tube and almost immediately branches into three veins which traverse the tube and enter the lobe unfused (fig. 1). The number of veinlets and degree of their fusion in the corolla lobe is of secondary importance and will not be considered.

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Navarretia subuligera deviates from the typical trinervate condition. In this species, the vein to the corolla lobe branches about one-third of the way up the corolla tube and enters the lobe unfused (fig. 2). This modification of the typical trinervate condition is of interest when compared with the vasculation of the remaining eight species.

The second series of plants comprising eight species shows a vascular pattern with a single vein traversing the corolla from the base of the tube to the lobe. Plants in this series will be referred to as uninervate. The single vein entering the corolla lobe becomes variously branched or remains unbranched, depending upon the species (figs. 3, 4, 5). The consistency with which such patterns occur within a single species or several merits attention developmentally and taxonomically.

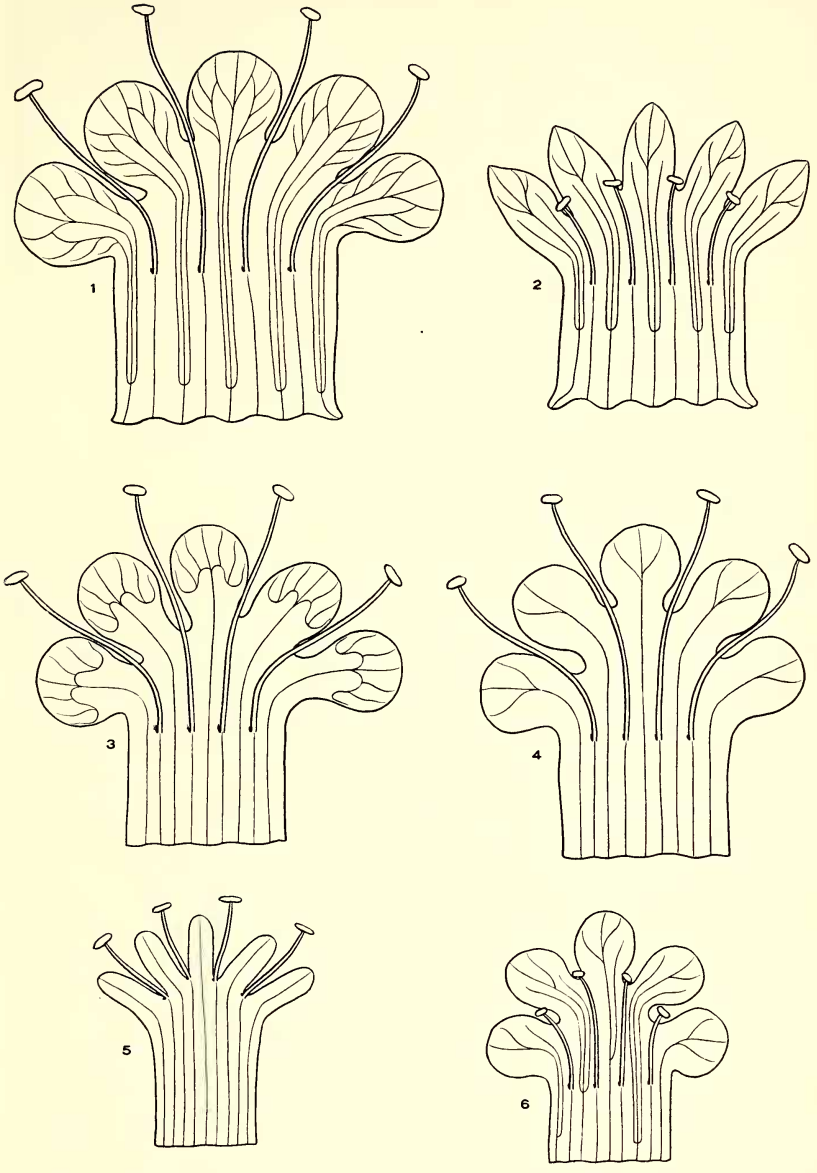
Among these uninervate species, *N. intertexta* retains a terminal corolla lobe pattern which is comparable to that of the trinervate species (fig. 3), a pattern which may be used to distinguish it from the closely related *N. propinqua* (fig. 4), wherein the two or three terminal veinlets in the corolla lobe are disposed divaricately. *Navarretia leucocephala* shows a similar pattern, but differs from *N. propinqua* in shape of the apex of the calyx membrane, stamen insertion, stigma lobing, and habitat. The remaining species in the uninervate series, *N. prostrata, N. minima, N. bakeri, N. plieantha,* and *N. pauciflora,* have a single unbranched vein traversing the entire corolla, from the base to the summit of the lobe and represent the ultimate reduction in corolla vasculation in the genus (fig. 5).

The only South American species, *N. involucrata,* although related to the uninervate series, is treated separately because of its exceptional and distinctive vasculation. Whereas the twenty-nine species of western North America are consistently either trinervate or uninervate, with no variations between these patterns, all Chilean collections of *N. involucrata* examined (*Morrison & Wagenknecht 17122, C. & G. Grandjot 3981, 3642, 1065, A. Donat 285*) showed variable reduction in vasculation within individual corollas on the same plant (fig. 6). This may be a consistent feature of this isolated species, and indicates an obvious specialization of vasculation directed towards the uninervate pattern from the trinervate.

2. Stamen Insertion

The concept of sympetalous corollas and epipetalous stamens involves a fusion of tissue of petals and staminal filaments to form the corolla tube and throat; from this tissue projects the unfused remainder of the anther-bearing filament. A remarkable series of positions of stamen insertion is evident in *Navarretia,* the different positions being definitely correlated with other structural features of the corolla.

In *N. mellita* the stamens are inserted nearly at the base of the corolla tube, leaving an exceptional long throat above (fig. 7). *Navarretia squarrosa,* a closely related species, shows the stamens to be inserted about or shortly below the middle of the corolla tube (fig. 8). In this regard, these



FIGS. 1–6. Types of corolla vasculation in *Navarretia*. FIG. 1. *N. mitracarpa* showing trinervate vasculation typical of the section *Eunavarretia* (corollas 7.5 mm. long). FIG. 2. *N. subuligera* (corollas 5.5 mm. long). FIG. 3. *N. intertexta* (corollas 6 mm. long). FIG. 4. *N. propinqua* (corollas 6 mm. long). FIG. 5. *N. plieantha* (corollas 5 mm. long). FIG. 6. *N. involucrata,* vascular pattern believed to be typical of this species (corollas 4 mm. long). The fifth stamen and its trace are not shown. Illustrations are semidiagrammatic.

two species are significant since they exhibit the lowest position of stamen insertion in any *Navarretia* corolla. A typical stamen insertion is exemplified by *N. pubescens* (fig. 9). For the most part, however, staminal insertion ranges from slightly above the middle of the corolla tube up to the sinuses of the corolla lobes. An evident correlation exists between the amount of corolla vasculation and the point of stamen insertion. The trinervate species generally have stamens inserted from near the base to about the middle of the corolla throat, except for those species which have unequal insertion with one or two stamens in the upper half of the throat. In the uninervate species, except for *N. intertexta* and *N. propinqua,* stamens are inserted above the middle of the corolla throat to the sinuses of the corolla lobes. All the uninervate species with a single unbranched vein supplying each corolla lobe have stamens inserted in or immediately below the sinuses of the corolla lobes (figs. 5, 10).

On the basis of this evidence it is concluded that there has been a definite migration of stamen insertion from near the base of the corolla to the very summit of the corolla tube, a migration correlated with progressive reduction of vasculation within the corolla.

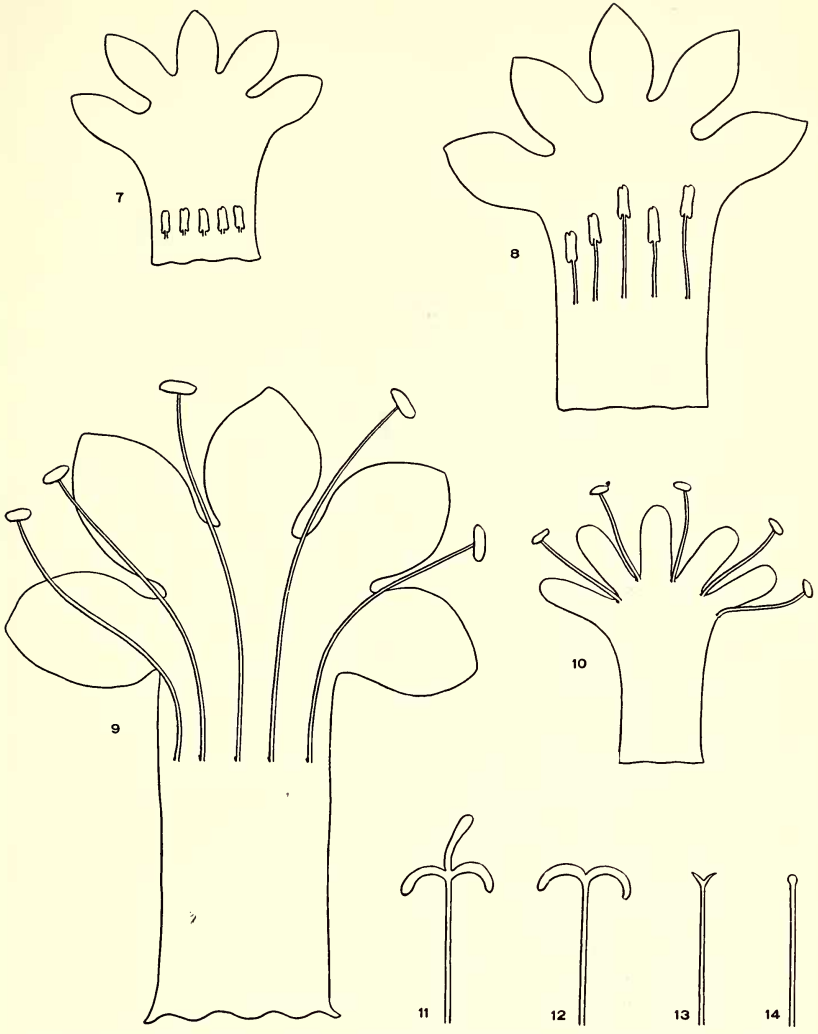
3. Stigma Lobing

In all trinervate species the stigmas are prominently 2- or 3-cleft (figs. 11, 12). Three-cleft stigmas are found in those species with 3-locular capsules, while 2-cleft stigmas occur with 1-2-locular capsules. The uninervate species with indehiscent capsules usually have minutely 2-lobed or entire stigmas (figs. 13, 14). Two exceptions, *N. intertexta* and *N. propinqua* retain a prominently 2-cleft stigma reminiscent of the trinervate species. Developmentally, the stigma has become modified from a deeply 3-cleft condition to one of entirety in coordination with capsular modification, and seemingly along with progressive reduction in corolla vasculation which is particularly evident in the uninervate species.

4. Capsule Modification

Greene (1887) remarked: "The astonishing range of variability in the capsule of *Navarretia* which will be brought to view in classification and description of species is almost something new in kind, in the annals of carpology, I think." Unquestionably capsule structure and behavior are highly important for classification and in understanding species interrelationships.

Two distinct phases of capsular structure and dehiscence are characteristic of *Navarretia*. The majority of the species have coriaceous, or chartaceous, dehiscent capsules, while the remainder are membranous, weak-walled, and indehiscent. The species with dehiscent capsules exhibit a variety of texture, structure, manner of opening, and except for *N. tagetina* and *N. subuligera,* release their seeds as discrete units. Four species, *N. squarrosa, N. mellita, N. heterodoxa* and *N. peninsularis,* have 3-celled coriaceous capsules which, upon dehiscence, split into three valves that



FIGS. 7–10. Types of stamen insertion in *Navarretia*. FIG. 7. *N. mellita,* note extremely short filaments; anthers are versatile (corollas 5 mm. long). FIG. 8. *N. squarrosa,* note filaments are longer than the anthers; anthers are versatile (corollas 10 mm. long). FIG. 9. *N. pubescens,* showing type of stamen insertion generally typical of section *Eunavarretia* (corollas 16 mm. long). FIG. 10. *N. bakeri,* stamen insertion in the sinuses of the corolla lobes (corollas 5 mm. long). FIGS. 11–14. Types of stigma lobing in *Navarretia*. FIGS. 11–12. Stigmas typical of the section *Eunavarretia*. FIGS. 13, 14. Stigmas typical of the section *Fragiles*. Illustrations are semi-diagrammatic.

separate from the top downwards, usually remain united at the base, and release six or more seeds from each locule. Six species, *N. hamata, N. atractyloides, N. viscidula, N. breweri, N. prolifera* and *N. divaricata,* possess 3-celled, coriaceous capsules that separate into discrete valves from the

base upwards, and release three to five seeds per locule. *Navarretia filicaulis* has become modified into a 2-celled, chartaceous capsule which splits, upon dehiscence, into two discrete valves, freeing 6 to 8 seeds. Six species, *N. pubescens, N. mitracarpa, N. jepsonii; N. heterandra, N. eriocephala* and *N. cotulaefolia,* are modified in another direction. The capsules disintegrate about the base, leaving a chartaceous "cap" enveloping the seeds. All are unilocular, 1-seeded, except for *N. pubescens,* which may also be 2-seeded and represent culmination in reduction of number of locules and number of seeds. The capsule of *N. nigellaeformis* is further modified by disintegration of the lower third, but remains 2-celled and releases 4 to 5 seeds. *Navarretia setiloba* capsules dehisce about the middle, are 1-celled and 1-seeded. This trend in progressive capsule disintegration culminates in two species, *N. tagetina* and *N. subuligera. Navarretia tagetina* retains a small chartaceous cap at the summit of the capsule; the remainder disintegrates and releases several coherent seeds. *Navarretia subuligera* is wholly membranous and does not regularly dehisce, but disintegrates leaving 3 or 4 coherent seeds. These two species retain three locules, even though the locule walls are thin; they also have the 3-cleft stigma.

With the exception then, of *N. tagetina* and *N. subuligera,* the weak-walled, membranous, indehiscent capsule is characteristic of those plants with uninervate corollas and forms the second biological type in *Navarretia.* The capsules of this type disintegrate at maturity releasing seeds as a slightly coherent unit in contrast to the regularly dehiscent type discussed above. While most of the species in this type are unilocular and several seeded, *N. leucocephala* and *N. prostrata* are many-seeded and possess a somewhat imperfectly 2-locular capsule. Occasionally, *N. pauciflora* may have a 1-seeded capsule.

It is concluded, in the light of the foregoing criteria, as well as evidence from the capsule, that the primitive capsule of *Navarretia* was 3-locular, coriaceous, and separated upon dehiscence into discrete valves releasing numerous seeds. A modification in structure and texture produced a 2-locular, chartaceous capsule. This, in turn, culminated in a capsule that is unilocular and 1-seeded with a papery or chartaceous envelope that disintegrates about the base upon dehiscence. *N. tagetina* and *N. subuligera* become transitional between regular dehiscence in the trinervate species and indehiscence in the advanced uninervate species.

5. Seed Number

Navarretia squarrosa, with 6 to 9 seeds per locule, has the largest number of seeds of any species. Seed number becomes progressively reduced, depending upon capsular modifications, and culminates in seven unilocular, 1-seeded species already mentioned. *Navarretia pubescens,* a member of this group, matures 1- and 2-seeded capsules within the same flowering head, but those with one seed are in the majority. As already discussed the trinervate species possessing regularly dehiscent capsules exhibit wide

variation between species as to the number of ovules matured. The indehiscent capsule of the uninervate species has a narrower range of seeds produced. *Navarretia leucocephala* and *N. prostrata* are many-seeded, probably 8 to 10 seeds per capsule, *N. minima* and *N. bakeri* are 4 to 5-seeded, *N. plieantha* is 2–4-seeded, and *N. pauciflora* is 1–4-seeded. *Navarretia intertexta* and *N. propinqua* are variable in the number of seeds usually maturing, about 4 to 8 per capsule. *Navarretia pauciflora* represents the culmination of reduction in seed number in this series of plants.

6. Glands

Along with other morphological criteria being considered, the prevalence of glands among *Navarretia* species appears to have important evolutionary significance. Unquestionably the heaviest concentration of glands upon the foliar and floral parts occurs in the trinervate species, *N. squarrosa, N. atractyloides, N. hamata, N. viscidula, N. mellita* and *N. heterodoxa*. The first four species are characterized by their strong mephitic odor, while the latter two are honey-scented and citrus-scented respectively. Glandular development decreases throughout the trinervate species and terminates with *N. subuligera* which is practically glabrous throughout. In this species a few scattered glands occur about the abaxial base of the bracts in the flowering heads. This glandless condition becomes very prevalent in the uninervate species which develop glands only on the abaxial base of the bracts and the calyx lobes. In some instances uninervate species may be entirely devoid of glands. It is apparent that a decrease in development of glands has to some extent followed progressive specialization of other plant structures and changes in habitat.

7. Vessel Anatomy

Stems from all species of *Navarretia* were macerated, and cleaned sections immersed from 6 to 12 hours, at room temperature, in a 10 per cent solution of nitric and chromic acids. The macerated wood was then stained with safranin in 50 per cent alcohol, passed through 50–100 per cent alcohol series, and permanently mounted in diaphane.

Examination of all species revealed some variation in vessel length and breadth. *Navarretia propinqua* has vessel elements averaging nearly 0.8 mm. in length and 0.019 mm. in width, by far the longest vessels found in any species, the closest rival being *N. involucrata* with an average of 0.7 mm. in length. The average and usual length of vessels in *Navarretia* is between 0.4 and 0.5 mm., the shortest being 0.25 in *N. tagetina*. All species have vessels with porous perforation plates. In *N. squarrosa,* however, both reticulate and scalariform[1] perforation plates commonly occur. There is some evidence that this condition may occur regularly in *N. atractyloides,* since several mounts of this species had a few vessels with scalariform perforation plates. Studies of anatomy by I. W. Bailey and his co-workers have indicated that scalariform and reticulate perforation

[1] Two to six bars are found in perforation plates of this type.

plates in vessels are more primitive than the derived porous condition. If this consideration is applied here in conjunction with evidence from other criteria, *N. squarrosa* is indicated as the most primitive species in the genus *Navarretia*.

Ecological Considerations

Two distinct groups of species may be recognized on the basis of ecological preference. The majority of species is found over a wide range of habitats which includes open plains, valley, meadow, or hillside, while a minority is confined in whole or part to vernal pools.

1. Varied Habitat.

Navarretia squarrosa ranges extensively along the Pacific Coast, rarely occurring very far inland, and particularly favoring cultivated or disturbed soil. It behaves as a ruderal in grain and other fields and along roadsides, but it is not rare to find stands of this species in hard-packed undisturbed soil. There is a tendency for the majority of these plants to be aggregated in areas with small pockets or depressions where water has stood during the spring. *Navarretia squarrosa* is remarkable for its long period of flowering, so that frequently on a single plant capsules ripen and dehisce while young heads continue to appear and flower. The long duration of anthesis from June to November, coupled with remarkable powers of rejuvenation following heavy injury, carries a suggestion of perennial behavior.

Navarretia mellita, a closely related species, occurs farther inland along the inner Coast Ranges of California, reaching its greatest development in association with chaparral. Frequently, however, it is found in disturbed soil along roadsides and occasionally on serpentine soils but never becomes weedy as does *N. squarrosa*.

Navarretia mitracarpa extends spottily from southern Oregon, through the inner Coast Ranges of California, to Santa Barbara County, reaching its greatest abundance in Monterey and San Luis Obispo counties. It reportedly occurs on serpentine soils, but whether exclusively or not requires further investigation. *Navarretia jepsonii* is especially partial to serpentine soil although it is not wholly restricted to it. Its range of distribution is from northern Napa County, California, into southern Lake County and east into western Colusa County. Most plants of *N. mitracarpa* and *N. jepsonii* appear to develop conspicuous reddish foliage and stems when found on serpentine. *Navarretia cotulaefolia* prefers meadow or even marshy conditions, occurring through the inner Coast Ranges of California and extending into the Sacramento Valley. *Navarretia divaricata* favors open pine forests and occurs in Idaho, southern Oregon, the mountains of the northern Coast Ranges of California, the Sierra Nevada, and in Santa Barbara County of California, at elevations of 4500–8000 feet. *Navarretia divaricata* subsp. *vividior* occurs from 1500–4000 feet in the northern Coast Ranges, Siskiyou and Modoc counties and south along the western slope of the Sierra Nevada to Mariposa County, and occupies

chaparral areas, roadsides, and open flats. *Navarretia breweri* prefers elevations of 5000–8000 feet, in open valleys, flats or meadows on the eastern slopes of the Cascades and Sierra Nevada mountains and extends generally throughout the Great Basin. Both *N. divaricata* and *N. breweri* are the only truly montane trinervate species and occur consistently above 4500 feet.

Navarretia setiloba is apparently restricted to the red clay soils in the vicinity of Havilah and Kernville, Kern County, in the southern Sierra Nevada in California. *Navarretia subuligera,* a comparatively rare species, appears to be endemic upon rocky, volcanic soils in the north Coast Ranges and in the northern Sierra Nevada of California, judging from the limited material and data available. This restriction to the specialized habitat of volcanic soils agrees with other marks of specialization shown by this highly advanced species.

Most of the species occurring on open plains and hillsides appear to be tolerant of edaphic variables and show no apparent preferences. Very often two or more species of *Navarretia* are found growing interspersed in similar situations in a relatively small area. H. L. Mason (oral communication) reports that eight distinct species are found growing together in a meadow in southern Lake County, California. *Navarretia intertexta* and *N. propinqua* are the only two species of the uninervate series which occur in varied habitats; all other species are trinervate.

2. The Vernal Pool Habitat.

The vernal pool habitat represents a major ecological specialization in *Navarretia*. Vernal pools range from small depressions in open plains, fields or valleys, to large swales that become filled with rain water in winter or early spring. Water gradually evaporates leaving either very hard packed soil, or, if the pools are very large, organic debris or peaty soil. Recession of the standing water encourages development of a flora whose members start development aquatically or in the muddy soil which later becomes hard and baked. Probably seeds of such *Navarretia* species germinate while still covered with water. *Navarretia leucocephala,* a common species in vernal pools of the Great Valley of California usually is found at the lowest point of the depression, suggesting aquatic germination; anthesis is reached before the soil has yet dried.

Six species, *N. bakeri, N. pauciflora, N. plieantha, N. prostrata, N. minima* and *N. leucocephala,* are confined almost exclusively to the vernal pool situations. Not only are these species very specialized ecologically, they are also all highly specialized morphologically having uninervate corollas, indehiscent capsules, entire or minutely 2-lobed stigmas, high stamen insertion and a paucity of glands. Peculiarities inherent to the vernal pool habitat may have influenced the development of an indehiscent capsule and reduction in glandulosity. The agglutinated seeds shed from the distintegrating capsule do not facilitate wide dispersal but this is not necessary in a limited habitat. The free seeds released by the de-

hiscent capsules of species in varied habitats insure dispersal over a wider area.

Glands, which probably restrict water loss to some degree, cease to be of value in a habitat which provides and holds within the soil sufficient water for the plant's demands regardless of loss through transpiration.

Navarretia intertexta, with indehiscent capsules and uninervate corollas, is basically allied to the vernal pool species. Ecologically, the species is exceptional in its wide tolerance of diversified habitats. It may be found on the edges of vernal pools, but is usually not an integral part of the vernal pool flora. More commonly it occurs on grassy plains, hillsides, meadows, dry creek beds or banks, roadsides, and even on serpentine soil. This is by far the most common species of *Navarretia,* having a wide range of distribution in California, Oregon, Washington, and Idaho. It frequently grows in association with other species, particularly *N. tagetina* and *N. pubescens.* While uninervate corolla, indehiscent capsule, and close association with the vernal pool habitat ally it with the uninervate series, the singular pattern of corolla lobe venation (fig. 3), the prominently 2-cleft stigma, the low stamen insertion, and the occurrence in varied habitats relate it to the larger trinervate series of species.

Navarretia propinqua, closely related to *N. intertexta* and often confused with it, occupies open plains, valleys, plateaus, and probably the edges of vernal pools. Principally a Great Basin species, it is found only east of the crest of the Cascade Mountains and the Sierra Nevada, where it has broad distribution in eastern Oregon, Washington, Idaho, Nevada, Utah, Colorado, and northern Arizona. *Navarretia intertexta* frequently occurs with it along the western and northern fringe of the Great Basin. The primary distinction between the two species is the pattern of corolla lobe venation (compare figs. 3 and 4).

The South American *N. involucrata* apparently occupies and is probably confined to vernal pools throughout the Andean Cordillera of Chile. One collection (*Morrison & Wagenknecht 17, 122*) refers to the species as growing, "in a small bog or vega, nearly dry." The indehiscent capsule and the specialized habitat link the species with the vernal pool group of western North America. However, the specialization in corolla vasculation (fig. 6), the 2-cleft stigma, and low stamen insertion mark the species as somewhat transitional between uninervate and trinervate groups.

Conclusions

Morphological and ecological evidence indicate two distinct developmental lines in the genus *Navarretia.* Two groups of species have been distinguished in *Navarretia* on the basis of corolla vasculation referred to as trinervate and uninervate, respectively. Other morphological and ecological features confirm separation of these two distinct developmental lines within the genus. It remains to assign sectional divisions to the genus. Brand (1907) first used the section *Eunavarretia,* which has been found to include many species with trinervate corollas, deep 2- or 3-cleft stig-

mas, low stamen insertion, and variable ecology. The sectional name *Eunavarretia* is thus appropriate for those species having these features. For the remaining nine species with uninervate corollas, indehiscent capsules, entire to 2-lobed stigmas, and shallow stamen insertion, which are generally confined to vernal pools, I propose a new sectional name.

Navarretia, sect. **Fragiles** sect. nov. Corollae lobi univenosi capsula membranacea irregulariter dehiscens stigma 2-scissum vel 2-lobatum vel integrum flores caerulei vel albi; plantae stagnis vernalibus restrictae. The species in this group are a somewhat homogeneous group of similar habitat and general superficial appearance, but closer morphological examination reveals significant differences. These differences are largely biological, each species showing advanced structural modifications over the older and well delineated species of *Eunavarretia*.

Three species are of unusual interest since they show evidence of transition between the two sections. Corolla vasculation, capsule dehiscence, and specialized habitat place *N. subuligera* intermediate between the *Fragiles* and *Eunavarretia*. *Navarretia intertexta*, on the basis of corolla vasculation, 2-cleft stigma, stamen insertion, and wide range of ecological preference is closer to *Eunavarretia*. *Navarretia involucrata* is perhaps the most unique of these transitional species since corolla vasculation alternates between uninervate and trinervate.

The most highly specialized species in the genus is *N. pauciflora*, a position it holds by virtue of its morphological reduction and its restriction to a vernal pool habitat. *Navarretia squarrosa* appears to be the most primitive member because of its almost perennial behavior, large seed number, and the nature of the vessels.

Much of the taxonomic confusion in *Navarretia* has been cleared up by Mason (1951) and his descriptions and key merit close attention in unravelling interrelationships within the genus. On the basis of the criteria discussed in this paper, an attempt has been made to further clarify these relationships and call attention to the evidence derived from various means of attack. The key presented here emphasizes these features and attempts to group the species according to their degree of specialization.

Key to the Sections and Species of Navarretia

A. Corolla lobes 1-veined; capsules membranous, indehiscent; stigmas entire, minutely 2-lobed, or 2-cleft; flowers pale blue or white; plants largely of vernal pools. Section 1. Fragiles

B. Stigmas entire or minutely 2-lobed; stamens inserted at mid-throat or above; calyx sinus-membrane truncate at summit; plants restricted to vernal pools.

C. Single vein in the corolla lobes unbranched; corolla lobes linear.

D. Stamens inserted in or immediately below the sinuses of the corolla lobes; flowers pale blue, rarely white.

E. Corolla exceeding the longest calyx lobes.

F. Plants erect, stems slender and branching from the base; heads few-flowered; stamens inserted immediately below the sinuses of the corolla lobes. 1. *N. pauciflora* Mason

FF. Plants prostrate, stems stoutish, proliferating from beneath a terminal head; heads many flowered; stamens inserted in the sinuses of the corolla lobes. 2. *N. prostrata* (Gray) Greene

EE. Corolla shorter than the longest calyx lobes.

G. Style slender, stigma 2-lobed, mature calyx with lobes nearly equal. 3. *N. plieantha* Mason

GG. Style stoutish, stigma entire to minutely 2-lobed; mature calyx with one lobe conspicuously longer than the others. 4. *N. bakeri* Mason

DD. Stamens inserted at mid-throat; flowers white. 5. *N. minima* Nutt.

CC. Single vein in the corolla lobes divaricatedly branched; corolla lobes ovate.

H. California 6. *N. leucocephala* Benth.

HH. South America 7. *N. involucrata* R. & P.

BB. Stigmas prominently 2-cleft; stamens inserted near the base of corolla throat; calyx sinus-membrane v-shaped at the summit; plants often bordering vernal pools but also in many diverse habitats.

I. Single vein of the corolla lobes divaricately branched into 2-3 veinlets; corollas usually subequalling calyx lobes. 8. *N. propinqua* Suksd.

II. Single vein of corolla lobes branched into 4–8 veinlets; corollas usually exceeding calyx lobes. 9. *N. intertexta* (Benth.) Hook.

AA. Corolla lobes 3-veined; capsules coriaceous or chartaceous, dehiscent, rarely indehiscent; stigmas prominently 2- or 3-cleft; stamens usually inserted at mid-throat or below; flowers blue, violet, pink, or yellow; plants of open plains, valleys, meadows, or hillsides. Section 2. Eunavarretia

J. Capsules not regularly dehiscent; stigmas 3-cleft, included; calyx with 2 very long and 3 very short lobes.

K. Bracts and calyx lobes almost glabrous; stamens included; flowers cream white. 10. *N. subuligera* Greene

KK. Bracts and calyx lobes coarsely villous; stamens exserted; flowers pale blue. 11. *N. tagetina* Greene

JJ. Capsules regularly dehiscent by valves; stigmas 2- or 3-cleft, included or exserted; calyx lobes variously unequal.

L. Capsules chartaceous, unilocular (rarely 2-locular); 1- 2-seeded; stigmas 2-cleft.

M. Capsules circumscissile near the base.

N. Corolla usually 4-merous.

O. Heads coarsely villous; stamens equally inserted just below the sinuses of corolla lobes; flowers yellow or cream colored. 12. *N. cotulaefolia* (Benth.) H. & A.

OO. Heads densely soft white-villous; stamens unequally inserted in throat; flowers blue or white. 13. *N. heterandra* Mason

NN. Corolla regularly 5-merous.

P. Capsules 4-valved; bract rachis expanded above or below.

Q. Corollas yellow or cream-colored, often with purple spots; bract rachis expanded below. 14. *N. eriocephala* Mason

QQ. Corollas purple, without purple spots; bract rachis expanded above.

R. Capsules 1- or 2-seeded, chartaceous throughout. 15. *N. pubescens* (Benth.) Hook.

RR. Capsules 1-seeded, thickened above along the sutures. 16. *N. mitracarpa* Greene

PP. Capsules 8-valved; bract rachis linear throughout. 17. *N. jepsonii* Bailey

MM. Capsules circumscissile at about the middle.
S. Capsules 1-seeded; flowers purple. 18. *N. setiloba* Coville
SS. Capsules 4–5 seeded; flowers yellow with purple spots.
19. *N. nigellaeformis* Greene
MMM. Capsules not circumscissile, incompletely 2-locular, separating into two halves upon dehiscence. 20. *N. filicaulis* (Torr.) Greene
LL. Capsules coriaceous, 3-locular, few to many-seeded; stigmas 3- cleft.
T. Capsules few-seeded, dehiscent from the base upwards.
U. Bracts palmate; branches proliferating from beneath terminal heads.
V. Plants coarsely villous; flowers to 1 cm. long, purple or yellow; stamens exserted. 21. *N. prolifera* Greene
VV. Plants glandular-puberulent; flowers up to 0.5 cm. long, pinkish; stamens included. 22. *N. divaricata* (Torr.) Greene
UU. Bracts pinnate-filiform throughout; branches basal or cauline.
23. *N. breweri* (Gray) Greene
UUU. Bracts expanded below, linear or lanceolate above.
24. *N. viscidula* Benth.
UUUU. Bracts broad-ovate below with terminal segments of 3 divergent, pungent lobes.
W. Stamens unequally inserted in throat; stigma included.
25. *N. atractyloides* (Benth.) H. & A.
WW. Stamens equally inserted in throat; stigma exserted.
26. *N. hamata* Greene
TT. Capsules many-seeded, dehiscent from the top downwards.
X. Corolla tube persistent, ruptured on one side by the maturing capsule.
27. N. *peninsularis* Greene
XX. Corolla tube circumscissile about the base and pushed upwards by the maturing capsule.
Y. Bracts broadly ovate at the base, digitately lobed above.
28. *N. heterodoxa* Greene
YY. Bracts narrow and often crowded at the base with many unequal acerose lobes.
Z. Plants slender, usually much branched; flowers pinkish; filaments shorter than the anthers and inserted near the base of the tube. 29. *N. mellita* Greene
ZZ. Plants coarse, usually little-branched; flowers blue-violet; filaments longer than the anthers and inserted near mid-tube.
30. *N. squarrosa* (Eschsch.) H. & A.

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Summary

1. Corolla venation is of two types, trinervate and uninervate, each one exhibiting progressive reduction.

2. Although the stamen vasculation is similar throughout the genus, stamen insertion shows migration from the base to the apex of the corolla and may be correlated with corolla venation.

3. The stigma shows a progressive reduction from the 3-cleft condition to one of entirety. This may be correlated with reduction in corolla vasculation.

4. The developmental trend in the capsule proceeds in two directions from a 3-locular, many-seeded, coriaceous structure. One direction has ended in a uni-locular, 1-seeded, chartaceous envelope having basal circumscissile dehiscence, while the other direction has terminated in indehiscent, thin-walled, several-seeded capsules. Correlation with corolla venation is less evident than elsewhere.

5. Vessel anatomy shows primitive vessels in species of little specialization.

6. Specialization in habitat is correlated with reduction in corolla venation, stigma lobation and staminal insertion.

7. Two sections of the genus, based upon morphological and ecological features, are accepted.

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CHROMOSOME NUMBERS IN SILENE (CARYOPHYLLACEAE): I.

A. R. Kruckeberg[1]

The genus *Silene* is represented in North America by fifty-four species, nine of which are introduced (Hitchcock and Maguire, 1947). All of the native perennial species, forty-two in number, are to be included in a current study of species interfertility and evolutionary relationships in the genus. In the course of this study, nineteen species of *Silene* and one of the closely related genus, *Lychnis,* have been examined cytologically. A summary of chromosome numbers (Table 1), camera lucida drawings of chromosome complements (figs. 1–28) and data on the cytological behavior of certain species and on the geographical source of the collected material are presented here.

The chromosome numbers were obtained primarily from acetic squash preparations of microsporocytes. Intact flower buds were fixed in three parts 95 per cent ethyl alcohol to one part glacial acetic acid and the anthers thus fixed squashed in acetocarmine. In cases where only pistillate plants of *Silene menziesii* Hook. were available, chromosome counts were made from aceto-orcein squashes of root tips or vegetative buds.

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